NITOPHYLLUM ADHAERENS SP. NOV. (DELESSERIACEAE, RHODOPHYTA) FROM THE CARIBBEAN AND BERMUDA

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ABSTRACT — *Nitophyllum adhaerens* sp. nov. is described from Quintana Roo, Caribbean Mexico, with supplemental reports of its occurrence from Puerto Rico (Greater Antilles), St Croix and St Kitts (Lesser Antilles), the Bahamas, and Bermuda. It has been collected both from shallow water (1-2 m depth) down to a depth of 61 m Distinctive characteristics of the new species include its relatively small stature (10-15 mm in extent), the frequent production of marginal rhizoids resulting in its firmly attached, epiphytic habit, and the restriction of the tetrasporangial and spermatangial sori typically to terminal lobes.

RÉSUMÉ — *Nitophyllum adhaerens* sp. nov. est décrit de Quintana Roo, Caraïbes Mexique, avec des indications supplémentaires de sa présence à Porto-Rico (Grandes Antilles), Sainte Croix et Saint Kitts (Petites Antilles), les Bahamas et les Bermudes. Il a été récolté dans des eaux peu profondes (1-2 m), mais aussi jusqu'à une profondeur de 61 m. Cette nouvelle espèce présente les caractéristiques distinctives suivantes: une taille relativement réduite (10-15 mm au total), la production fréquente de rhizoïdes marginaux qui lui permettent de s'ancrer solidement, d'être épiphyte et de posséder des sores de tétrasporocystes et de spermatocystes typiquement présents sur les seuls lobes terminaux. (Traduit par la Rédaction)

KEY WORDS: Caribbean, Delesseriaceae, marine algae, *Nitophyllum*, *N. adhaerens*, Rhodophyta

INTRODUCTION

Recent floristic accounts of benthic marine algae from the tropical and subtropical western Atlantic have included *Nitophyllum punctatum* (Stackhouse) Greville and *N. wilkinsoniae* Collins & Hervey (Wynne, 1986). Some reports of the former species (Harvey, 1853; Taylor, 1942) have later been questioned (Schneider & Searles, 1991), and some reports of the latter species have later been re-identified to be *Myriogramme distromatica* Boudouresque (Schneider & Searles, 1991). Other species that had at one time been included in a broadly circumscribed *Nitophyllum* have later been placed in segregate genera, such as *N. medium* Hoyt now placed in *Calonitophyllum* (Aregood, 1975) and *N. lenormandii* (Derbès & Solier) Rodriguez now placed in *Haraldia* (Feldmann, 1939).

Several collections of an alga that fits *Nitophyllum* on the basis of its vegetative structure and the organization of its female plants have been made from scattered locations in the tropical/subtropical western Atlantic. This alga appears to represent an undescribed species. Its delineation from the known species of *Nitophyllum* as well as other small Delesseriacean species with which it might be confused is the subject of this paper.

MATERIALS AND METHODS

Collections, which were made either by snorkeling in shallow depths or by SCUBA at relatively greater depths, were preserved in 5 % formalin-seawater solution. Specimens of the *Nitophyllum* were usually found as rather inconspicuous epiphytes on coarser algae and picked off the hosts. Material was then placed on glass slides and stained with 1 % aniline blue acidified with dilute acetic acid. After the mounts were rinsed of excess stain, they were ringed with liquid glucose (Karo corn syrup) and placed in a warming oven to solidify. Some material was processed on the slides but not stained. A standard Zeiss research microscope equipped with a camera lucida was used to prepare the illustrations. Loans of specimens were received from Dr D. L. Ballantine (MSM), US, and from the private herbarium of Dr C. W. Schneider. Herbarium abbreviations follow Holmgren *et al.* (1990).

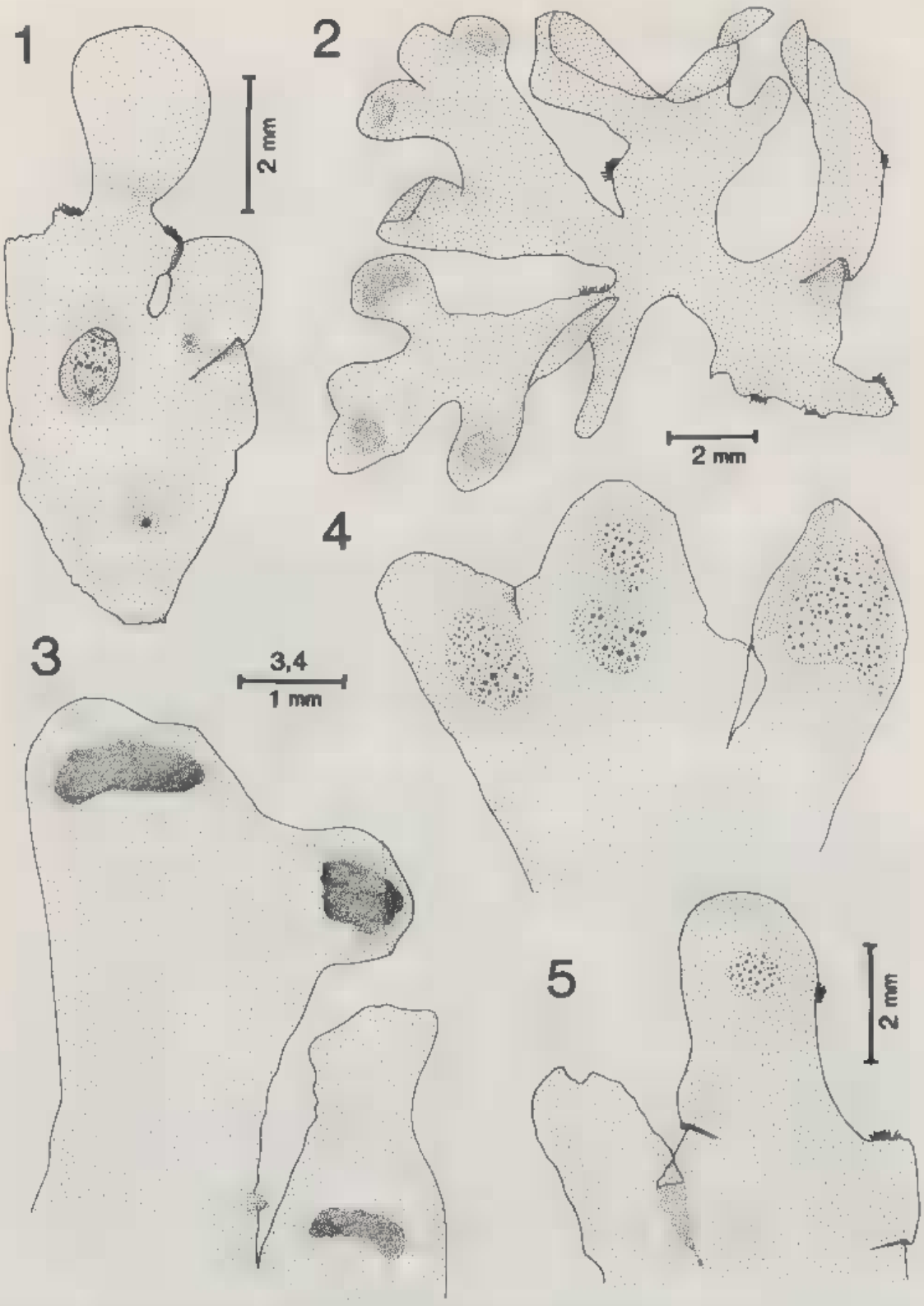
OBSERVATIONS

Vegetative structure

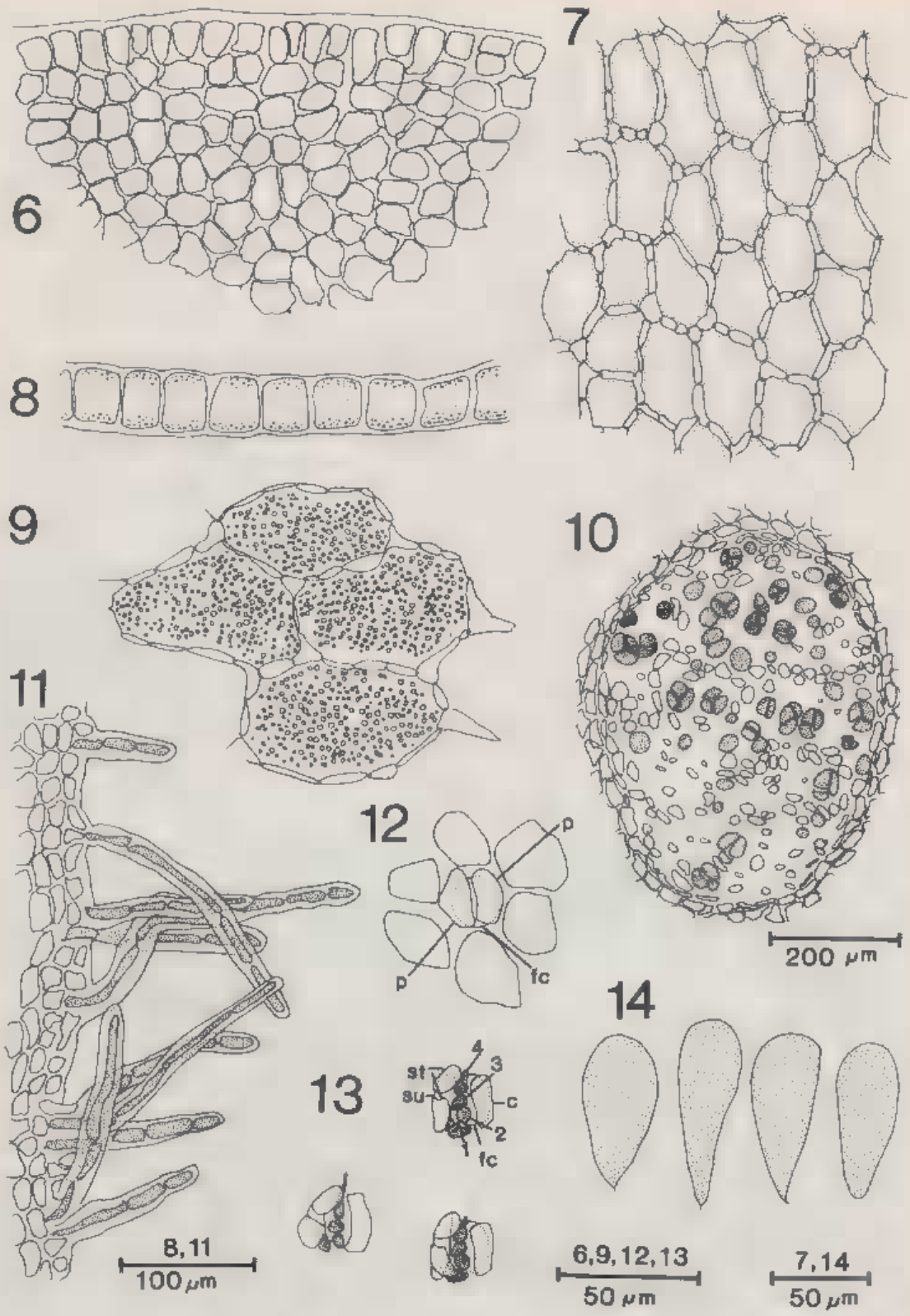
Thalli are very delicate blades (Figs 1-5) tending to sprawl over and become firmly attached to the substrate, which are typically coarse algae such as *Halimeda scabra* Howe and *Gracilaria* spp., but can also be entangled with relatively small *Jania adhaerens* Lamouroux. In overall extent, thalli reach no more than 10-15 mm, and individual blades are 1.8-3.0 (-4.0) broad. Terminal segments are generally only 1.0 mm broad. Growth is by marginal initials undergoing oblique segmentation (Fig. 6). Blades are essentially monostromatic (Fig. 8) but are occasionally distromatic in basal portions; there are no macroscopic or microscopic veins. Blades are about 40-45 µm in thickness in distal regions and up to 60 µm in more proximal portions. Blade margins are entire, but they are frequently interrupted by the production of marginal rhizoids (Figs 1-2), both arising singly or in clusters (Fig. 11). Individual rhizoids can be unicellular or multicellular. These rhizoids result in the blades becoming strongly adherent to the substrate as well as mutually connate and entangled, such that attempting to dislodge them results in the blades being easily torn. Mature cells of the blades are variable but are typically elongate (Fig. 7), measuring 56-64 µm (range of 50-86 µm) in length and approximately 20-38 µm in width. Adjacent cells are linked together by frequent secondary pit-connections. The cells contain numerous small discoid chloroplasts, scattered at the surfaces of the cell (Fig. 9).

Reproductive structure

Although vegetative thalli are usually closely attached to the substrate and become secondarily attached whenever and wherever blade margins come in contact with



Figs 1-5. *Nitophyllum adhaerens*. Fig. 1. A female thallus bearing a mature cystocarp and a pair of young post-fertilization stages. Figs 2-3. Spermatangial thalli. Figs 4-5. Portions of tetrasporangial thalli.



Figs 6-14. *Nitophyllum adhaerens*. Fig. 6. Growing margin of blade with dividing initials. Fig. 7. Mature cells of blade with pit-connections linking adjacent cells. Fig. 8. Cross-section of portion of blade. Fig. 9. Surface view of cells of blade, showing numerous small chloroplasts. Fig. 10. Tetrasporangial sorus. Fig. 11. Production of rhizoids from blade margin. Fig. 12. Immature procarp showing a pair of pericentral cells (p) associated with a fertile central cell (fc). Growing margin is toward top of page. Fig. 13. Examples of procarps, in which one pericentral cell has become a supporting cell (su) bearing a four-celled carpogonial branch (1,2,3,4) and a sterile-cell group (st), and the other pericentral cell is serving as a cover cell (c). Fig. 14. Individual carposporangia.

substrate or with self, reproductive organs are often borne on the non-attached terminal lobes of blades. Female thalli bear randomly scattered procarps and resultant cystocarps over the blade surface (Fig. 1). The pattern of development of the procarp is in conformity with that as shown in the genus by Kylin (1924) and more recently by Millar (1990). A fertile central cell cuts off a pair of pericentral cells to each surface of the blade (Fig. 12). Typically, a procarp is developed on only one side of the blade surface, the dorsal surface. The instance of the development of a procarp (*i.e.*, carpogonial branch and associated sterile cells) on both sides of a fertile central cell was observed. The pericentral cells are arranged such that an axis drawn through them lies perpendicular to the longitudinal axis of the thallus. One of these pericentral cells becomes the cover cell of the procarp; it may undergo subsequent cell divisions. The other pericentral cell serves to produce the four-celled carpogonial branch as well as a sterile cell (Fig. 13). Cystocarps are covered by a simple, ostolate, dome-shaped pericarp (Fig. 1). Mature pericarps measure 650-860 µm in diameter. Carposporangia are produced terminally on a tuft of radiating gonimoblast filaments. The mature teardrop-shaped carposporangia (Fig. 14) are 56-86 µm in length and 32-42 µm in diameter.

Male thalli (Figs 2-3) produce spermatangial sori in circular to ovate patches usually located in terminal lobes or in the proximity of blade margins. These sori tend to be discrete and relatively small.

Tetrasporangiate thalli (Figs 4-5) bear circular to ovate sori, typically singly in terminal lobes of the thallus. Occasionally two or three smaller discrete sori will be present in close proximity. The tetrasporangia are produced in several layers within the sorus (Fig. 10) and are released to both surfaces of the blade. The tetrasporangia are tetrahedrally divided and measure 38-50 (-54) µm at maturity.

Nitophyllum adhaerens M. J. Wynne sp. nov.

Nitophyllum cum laminis delicatis monostromaticis, venas destitutum, irregulariter vel dichotome ramosum vel lobatum, parva statura distinctum: 1.8-3.0 (-4.0) mm lata atque 10-15 mm longa, rhizoidea marginalia saepe producens, habitum adhaerentem epiphyticum firme efficiens, et sori tetrasporangiferi atque spermatangiferi ad lobus terminales typice restricti.

Diagnosis: Delicate monostromatic blades, lacking veins, irregularly or dichotomously branched or lobed, distinguished by its small stature: 1.8-3.0 (-4.0) mm broad and 10-15 mm long, the frequent production of marginal rhizoids, resulting in its firmly attached, epiphytic habit, and the restriction of the tetrasporangial and spermatangial sori typically to terminal lobes.

Holotype: *M.J. Wynne 9605* (herbarium specimen and mounted slides in MICH); male, female, and tetrasporic; 3-4 m depth. 24.v.1992, Bocana Reef off of Estacion Puerto Morelos, State of Quintana Roo, Mexico.

Isotypes: slides deposited in MEL, PC, UC, US.

Additional collections: MEXICO. State of Quintana Roo. Bocana Reef off of Estacion Puerto Morelos: 24.v.1992. *M.J. Wynne 9671* (female, male, tetrasporic; epiphytic on *Halimeda scabra* and *Jania adhaerens*), *M.J. Wynne 9686* (male, tetrasporic; epiphytic on *Gracilaria* sp.); Ojo de Agua, Puerto Morelos: 25.v.1992, *M.J. Wynne 9696* (female; 1.5 m depth); coral reef 2 km north of Estacion Puerto Morelos: 26.v.1992, *M.J. Wynne 9716* (male; 2 m depth).

PUERTO RICO, GREATER ANTILLES. North coast at Islote, near Arecibo: 12.vi.1991, *D.L. Ballantine 4818* (18 m depth, SCUBA collection). Punta Aguje-

reada, Aguadilla: 13.vi.1991, *D.L. Ballantine 4219* (18 m depth, SCUBA collection). Edge of insular shelf off Salinas: 9.xii.1983, *D.L. Ballantine 1435* (tetrasporic; 32 m depth; on sponges).

ST KITTS, LESSER ANTILLES. Half Moon Bay: 23.xi.1995, *M.J. Wynne 10456* (male; 2 m depth, epiphytic on *Jania* sp.).

U. S. VIRGIN ISLANDS. Boiler Bay, St Croix: 18.i.1974, *R. Steneck 11749* (tetrasporic; on *Caulerpa racemosa* in drift; US 089371).

BAHAMAS. Lee Stocking Island: i.1995, *D.L. Ballantine 4964* (61 m depth).

BERMUDA.The Spit, northeast of Little Head, St David Island (32° 22.4′ N, 64° 38.5′ W): 19.vi.1985, *C.W. Schneider & R.B. Searles 85-23-20* (1-12 m depth). Jacks Flats, east of St. George's Island (32° 23.1′ N, 64° 38.0′ W): 7.viii.1983, *C.W. Schneider & R.B. Searles 83-8-9* (15-18.5 m depth).

DISCUSSION

Nitophyllum Greville, with about 30 recognized species, has a wide distribution in warm temperate to tropical seas of both Northern and Southern Hemispheres. In its currently more narrowly circumscribed definition (Kylin, 1956), *Nitophyllum* is characterized by a vegetative organization of blades that are typically delicate, undivided, lobed, or regularly or irregularly divided, with distal monostromatic portions and proximal polystromatic portions. A midrib and macroscopic or microscopic nerves are entirely absent. Growth takes place by means of many marginal initials undergoing oblique divisions. Its female reproductive organization consists of procarps (and resultant cystocarps) that have a randomly scattered arrangement over the entire blade surface. A fertile cell on a female blade produces two pericentral cells lying side by side (their axis is perpendicular to the long axis of the thallus). One of these pericentral cells serves as a cover cell (which can subsequently become divided) and the other becomes a supporting cell, giving rise to a four-celled carpogonial branch and one group of sterile cells. Carposporangia are produced singly (terminally) on the tips of the gonimoblast filaments of the carposporophyte. The spermatangial and tetrasporangial sori also randomly scattered over blade surfaces of male and tetrasporangiate thalli, respectively. Many species had been assigned to *Nitophyllum* when it was a broadly circumscribed genus (Agardh, 1876, 1898; DeToni, 1900; Lucas, 1926), but with a more narrow definition (Kylin, 1956) it came to include fewer species. Yet even now some of the species still placed in the genus need to be re-examined to determine if their placement is correct.

Despite the more restricted circumscription of *Nitophyllum*, the species herein being described does conform in both its vegetative and reproductive characteristics to this genus. *Nitophyllum punctatum*, the lectotype of the genus, generally has a European-based distribution, occurring from Norway to Morocco as well as the Mediterranean, Black, and Aegean Seas (Feldmann, 1941; Funk, 1955; Ardré, 1970; Athanasiadis, 1987; Maggs & Hommersand, 1993). It has been reported to occur in India (Silva *et al.*, 1996), the West Indies, Venezuela (Taylor, 1942), and Florida (Harvey, 1853; Woelkerling, 1976). Although Schneider & Searles (1991) excluded the occurrence of *N. punctatum* from the domain of their flora, ranging from North Carolina to northern Florida, Phycotheca Boreali-Americana no. 747 ["*Nitophyllum punctatum* var. *ocellatum* (Lamour.) J. Ag."] from both Indian River Inlet, which is north of Cape Canaveral, and Jupiter Inlet, Florida, appears to be genuine *N. punctatum*. Thalli of *N. punctatum* are very thin, erect blades, often reaching 50 cm in height, usually regularly dichotomously branched and

possibly deeply cleft into two or several principal segments (Harvey, 1847, pls 102 & 103; Hiscock, 1986; Maggs & Hommersand, 1993). Tetrasporangial sori have a scattered arrangement over both blade surfaces; the sori typically have an elliptical or elongate outline. The much larger size of the thalli, their erect habit, and the general distribution and shape of the tetrasporangial sori distinguish *N. punctatum* from *N. adhaerens*.

The species in the flora of the tropical-subtropical western Atlantic that bears some resemblance to the new species is *Nitophyllum wilkinsoniae* Collins & Hervey (1917). Phycotheca Boreali-Americana no. 2037 is regarded as syntype material. Earlier thought as an endemic to Bermuda (Howe, 1918; Taylor, 1960), *N. wilkinsoniae* has been reported to occur in Venezuela (Ganesan, 1983) and Florida (Hanisak & Blair, 1988), whereas reports attributed to this species from North and South Carolina (Wiseman & Schneider, 1976) were later identified as *Myriogramme distromatica* Boudouresque [see below]. Thalli of *N. wilkinsoniae* reach a larger size (to 10 cm in height) than in *N. adhaerens*, and individual blades can be up to 10 mm wide; they are essentially erect, although densely tufted. The margins of the blades are densely beset with small ciliform teeth (Collins & Hervey, 1917) or sparingly erose-dentate (Taylor, 1960).

A "*Nitophyllum* sp.", reported from a 74 m depth off the west coast of Barbados (Macintyre *et al.*, 1991), remains to be examined. It was not fertile. Bula Meyer (1986) reported a "*Nitophyllum* sp." from the Caribbean coast of Colombia, which he also tentatively regarded as *N. marmoratum* Rodriguez, a species known only from the Mediterranean. *Nitophyllum marmoratum* is a monostromatic blade with a deeply lobed, entire margin, attached by a single conspicuous stipe. The presence of microscopic veins and of many small discrete tetrasporangial sori scattered over the blade surface clearly separate it from *N. adhaerens* (Rodriguez, 1889).

Funk (1955) described two new species of *Nitophyllum* from the Bay of Naples, *N. micropunctatum* and *N. rotundum*. The former species, occurring usually at depths of 10-30 m but also at only 0.5 m depth, was described as showing a superficial similarity to *N. punctatum* but with a more elegant organization and larger-sized cells. It displayed a very bright iridescence, and its chloroplasts were arranged in chains. Tetrasporangial sori were small, each containing just a few tetrasporangia. *Nitophyllum rotundum*, on the other hand, was described on the basis of fragments of thallus, 5 cm long and equally broad, with relatively large cells. Male thalli were the only reproductive stages observed, and the sori were intermixed with vegetative cells such that the sori appeared to overlap. The fact that this species was collected from a depth of approximately 50 m was regarded as an additional distinction. Clearly, *N. adhaerens* is separable from these two Mediterranean species.

Nitophyllum marginale (Kütz.) J. Agardh (1876), first described as *Aglaophyllum marginale* by Kützing (1869) from Ceylon (= Sri Lanka), shares some similarities to the new species, such as its habit of delicate, dichotomously branched, deeply lobed blades. But the blade margins in *N. marginale* bear conspicuous teeth, and the cystocarps also are borne from the blade margins. According to Krishnamurthy & Varadarajan (1991), thalli of *N. marginale* reach 8-10 cm in height and have blade lobes 2-3 cm in breadth, dimensions much greater than those in *N. adhaerens*.

In Cribb's (1983) report of *Nitophyllum tongatense* Grunow (1874) from the Great Barrier Reef, he depicted a small (2 cm long) membranous alga with a prostrate or subprostrate habit, resembling *N. adhaerens* in many of its features. Mature blades of *N. tongatense*, however, becomes three cell layers in thickness, which is not true of the blades of the new species. In a paper on the iridescence displayed by material of *N. tongatense*

from Sri Lanka, Svedelius (1909) described the cells as containing a small number of deeply lobed plates or bands.

Nitophyllum delicatum, which was described by Millar (1990) from the vicinity of Coffs Harbour, New South Wales, Australia, is a flabellate, membranous plant, to 6 cm in height, irregularly branched or lobed, the lobes being deeply rounded, and with a sessile attachment or with a cartilaginous stipe. Although upper portions of the blades are monostromatic, basal portions become considerably thicker.

In turning our attention to other members of the Delesseriaceae in this same geographical region with which the new species might show some resemblance, we should consider *Myriogramme distromatica* Boudouresque (1971), an alga which had been first noticed from the western Mediterranean (with the manuscript name *Nitophyllum distromaticum*) by J. J. Rodriguez. Schneider & Searles (1991) reported it from deep-water collections from both North and South Carolina and indicated that it had been initially mis-identified as *Nitophyllum wilkinsoniae* (Wiseman & Schneider, 1976). The small size of the blades (to 1.5 cm long in the Mediterranean material and to 3.5 cm long in the Carolinian material), their lack of veins, and their creeping habit are shared features with *N. adhaerens*. But other features easily distinguish *M. distromatica*, such as the distromatic nature of the blades and their dorsiventrality, the production of rhizoids from the ventral surface, and the presence of a single lobed chloroplast in each cell (in contrast to numerous small discoid chloroplasts in *N. adhaerens*). The fact that reproductive specimens have yet to be discovered makes the generic placement of *M. distromatica* equivocal. Also, the cytological features would indicate that it bears no relationship to either *Nitophyllum* or *Myriogramme* (Maggs & Hommersand, 1993).

Myriogramme prostrata (E.Y.Dawson *et al.*) M.J.Wynne has been reported from Caribbean Costa Rica (Wynne, 1990) in addition to its original location of Baja California, Pacific Mexico (Dawson *et al.*, 1960). Its prostrate habit, production of many rhizoids from blade margins, and the marginal location of tetrasporangial sori are similarities with *Nitophyllum adhaerens*. The presence of conspicuous marginal teeth, with transversely dividing apical cells, present in *M. prostrata* serve to distinguish it from *N. adhaerens*.

Because of its often creeping and entangled habit, *Haraldia lenormandii* (Derbès & Solier) Feldmann is another Delesseriacean that might be confused with *Nitophyllum adhaerens*. The distribution of *H. lenormandii* is now known to include Bermuda and off shore Georgia (Wynne, 1990). Thalli of *H. lenormandii* are delicate monostromatic blades and grow usually attached or entangled with other algae, growing over their hosts and becoming sessile by producing marginal rhizoids and denticulations strongly anchoring them to the substrate. Veins and nerves are entirely lacking. *Haraldia* can be easily distinguished from *Nitophyllum* by its growth from a single transversely dividing apical cell and the production of both tetrasporangial and spermatangial sori that occupy a median location on the blade (Feldmann, 1939). These sori may remain discrete or become coalesced into a more or less continuous median sorus (Wynne, 1990).

Drachiella minuta (Kylin) Maggs & Hommersand is another delesseriacean species with some resemblance to *Nitophyllum adhaerens* primarily because of its small stature and growth by means of marginal initials. This species, earlier known as *Myriogramme minuta* Kylin (1924), was transferred to *Drachiella* by Maggs & Hommersand (1993) primarily on the basis of its distinctive cytology. Magne (1957) observed that the single chloroplast per cell in this species results from the fusion of several chloroplasts, which was the first such demonstration of this occurring in the Rhodophyta. The condition of numerous small chloroplasts in each cell of *N. adhaerens* easily separates it from *Drachiella*.

Myriogramme carnea (Rodriguez) Kylin, which was originally described by Rodriguez (1889) from Menorca in the western Mediterranean, has been reported from the Great Barrier Reef by Cribb (1983). Cribb's description of this species, as being membranous, prostrate or subprostrate, to 1.5 cm long, irregularly subpalmately to dichotomously lobed or branched and being one cell thick throughout are features very much reminscent of *Nitophyllum adhaerens*. Cribb refers to this Australian alga as being attached by multicellular rhizoids here and there on undersurface and margins. Rhizoids are produced from the margins in *N. adhaerens*, although their production from the undersurface of the blade has not been observed to occur. When one checks Rodriguez' (1889, as *N. carneum*) original account of this species, one sees that his alga was an erect bladed alga with a pronounced simple or bifurcate stipe. Mature thalli reached 4 to 9 cm in height, and Rodriguez stressed the fact that the blade showed rigidity, such that a specimen, when held by its stipe, remained erect without bending from its weight. This original account of *M. carnea* depicts an alga very different from both *N. adhaerens* and the alga portrayed as *M. carnea* by Cribb (1983).

There are some similarities between *Nitophyllum adhaerens* and *Myriogramme goaensis*, which was described from Goa, India, by Krishnamurthy & Varadarajan (1990; validated in Krishnamurthy, 1992) in regard the small size of the blades, the absence of any veins, and the production of tufts of rhizoids from the blade margins. The mature thallus in the Indian alga, however, is three cells in thickness, and the blade margins have teeth-like projections terminated by transversely dividing apical cells, both features not occurring in *N. adhaerens*.

A small bladed alga from the Mediterranean was depicted by Coppejans (1983) as "*Myriogramme unistromatica* sp. nov. ined." Its veinless, monostromatic blades, growth by marginal obliquely dividing initials, and formation of rhizoids from the blade margin are shared features with *Nitophyllum adhaerens*. But the pattern of distribution shown in both the spermatangial and tetrasporangial sori and the presence of a single lobed chloroplast in each cell clearly separate this undescribed Mediterranean taxon from *N. adhaerens*.

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